

## Forum

### Beyond spatial overlap: harnessing new technologies to resolve the complexities of predator–prey interactions

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Predation risk, the probability that a prey animal will be killed by a predator, is fundamental to theoretical and applied ecology. Predation risk varies with animal behavior and environmental conditions, yet attempts to understand predation risk in natural systems often ignore important ecological and environmental complexities, relying instead on proxies for actual risk such as predator–prey spatial overlap. Here we detail the ecological and environmental complexities driving disconnects between three stages of the predation sequence that are often assumed to be tightly linked: spatial overlap, encounters and prey capture. Our review highlights several major sources of variability in natural predator–prey systems that lead to the decoupling of spatial overlap estimates from actual encounter rates (e.g. temporal activity patterns, predator and prey movement capacity, resource limitations) and that affect the probability of prey capture given encounter (e.g. predator hunger levels, temporal, topographic and other environmental influences on capture success). Emerging technologies and statistical methods are facilitating a transition to a more spatiotemporally detailed, mechanistic understanding of predator–prey interactions, allowing for the concurrent examination of multiple stages of the predation sequence in mobile, free-ranging animals. We describe crucial applications of this new understanding to fundamental and applied ecology, highlighting opportunities to better integrate ecological contingencies into dynamic predator–prey models and to harness a mechanistic understanding of predator–prey interactions to improve targeting and effectiveness of conservation interventions.

Keywords: encounter rates, home range overlap, predation risk effects, predation sequence, predator–prey interactions, spatial ecology

## Introduction

Understanding predator–prey interactions is a cornerstone of ecology, with implications for individual fitness and population dynamics of both predators and prey, as well as community structure and ecosystem function (Sih et al. 1985, Krebs et al. 1995, Schmitz 2010). The risk of predation (i.e. the probability that a prey animal will be killed by a predator) is a major determinant of predator effects on prey and thus central to everything from classical predator–prey theory to the applied management of animal populations (Berryman 1992, Vucetich et al. 2011, Gaynor et al. 2020). The validity of theoretical predictions and the ability to anticipate the outcomes of management actions (e.g. predator removal, changes in hunting regulations) therefore rests on the accuracy of predation risk estimates. Decades of theoretical and experimental work show that predation risk varies dynamically with predator and prey behavior (Sih 1984, 2005, Krebs et al. 2001) and, for a given predator–prey pair, is likely to be context-dependent, contingent on predator motivation (e.g. availability of alternative prey; Stephens and Krebs 1986), prey resource availability (e.g. spatial anchors; Smith et al. 2019a), and/or local environmental conditions (e.g. distribution of refuge habitat; Wirsing et al. 2010). Given these complexities, studies of predator–prey interactions have often used proxies for the risk of predation that can be readily measured in field situations with mobile or cryptic animals (Moll et al. 2017, Prugh et al. 2019). Spatial overlap between predators and prey has emerged as a common metric (Schmitz et al. 2017), being both a necessary prerequisite to any predation event and relatively easy to calculate from available data sources such as predator and prey surveys or GPS locations. However, the degree to which spatial overlap serves as a valid proxy for predation risk rests on a series of assumptions that have often been overlooked and

unvalidated in predator–prey research, particularly research involving medium- to large-bodied vertebrates.

Predation itself is the culmination of a sequence of events (i.e. the predation sequence; Lima and Dill 1990, Endler 1991) that begins with spatial overlap between predators and prey and progresses through encounter, attack and prey capture and consumption (Fig. 1). Importantly, spatial overlap does not imply encounter, which we define here as a situation in which predator and prey are within the detection range of one or both participants, and one or both individuals detect the other. The predation sequence can end at any of the above stages if predator and prey fail to encounter each other or if the predator forgos, abandons, or is unsuccessful in a predation attempt. Predation risk, then, is a function of the rate at which a prey animal encounters its predators and the probability of capture given an encounter (i.e. conditional capture probability, CCP) (Hebblewhite et al. 2005). We suggest that a detailed, mechanistic understanding of these two values – encounter probability and CCP – is key to accurately estimating predation risk.

In the simplest scenario, predators are more likely to encounter prey when spatial overlap is high, leading to higher risk of predation if CCP is constant. In such cases, estimating overlap between predators and prey will indeed provide useful information on encounters and the likelihood of a predation event. However, even in this simple scenario, assumptions regarding the spatial scale and time period over which overlap is estimated, relative to the instantaneous conditions within which predator–prey encounters actually occur, can influence the correlation between overlap estimates and true predation risk (Hammond et al. 2012). Additionally, variation in CCP may weaken the correlation between encounters and predation events (Fig. 1). The predation sequence can end post-encounter based on decisions made by either predator or prey (Sheriff et al. 2020b, Wootton et al. 2021)

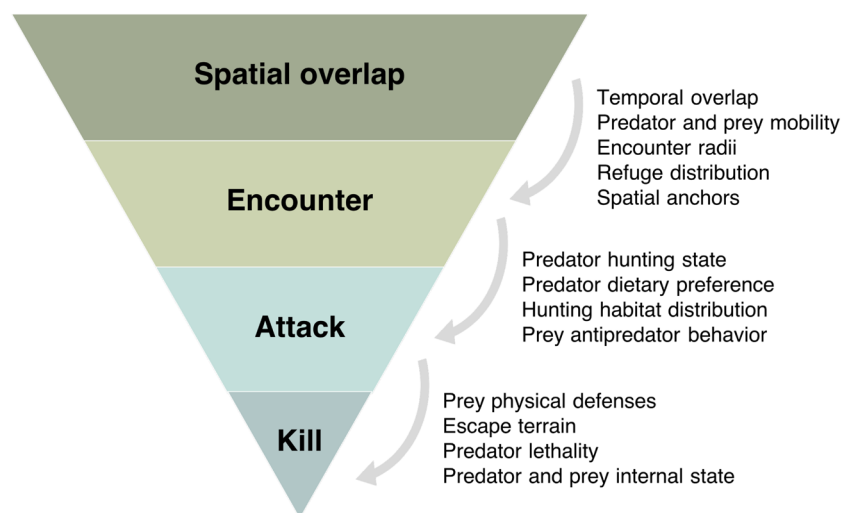


Figure 1. Factors that influence the relationship between stages of the predation sequence. The predation sequence is hierarchical, whereby events at later stages are rarer and dependent on previous stages. Conditions associated with predator and prey identity, predator and prey state, and environmental variation each influence the likelihood that one stage will progress to a subsequent stage.

and aspects of both species biology and the environment that affect energetic state, defense efficacy, and/or hunting performance (Guiden et al. 2019). Until recently, limitations in monitoring technologies have forced many of these complexities to be overlooked in free-ranging populations, despite an appreciation for the context-dependencies of interaction strength (Chamberlain et al. 2014) and the disconnect between overlap and predation mortality (Lichtenstein et al. 2019) in laboratory-based predator–prey experiments.

The rapid development of new technologies for remotely monitoring wildlife behavior and space use (e.g. biologging and remote sensing; Allan et al. 2018, Williams et al. 2020), and advanced statistical approaches to handle complex data sets (e.g. hierarchical models and classification methods; Gurarie et al. 2016, Rota et al. 2016, Hooten et al. 2019), provide greater ability to disentangle important complexities in predator–prey interactions. However, scientific inertia has kept the focus within predator–prey research, particularly among medium- and large-bodied vertebrates, on quantifying the probability of spatial overlap between predator and prey (Say-Sallaz et al. 2019). Here, we make the argument that the disconnects between spatial overlap and predation risk are numerous and pervasive, precluding accurate estimation of the risk experienced by prey through the quantification of space use or habitat selection alone. Furthermore, we propose adoption of technological advances to examine predator–prey interactions across the predation sequence, rather than isolating individual stages as proxies for risk or interaction strength.

In this paper, we focus on medium- and large-bodied vertebrates for the following reasons: 1) Recent reviews have suggested that the range of metrics of predation risk in free-ranging large vertebrates vary in their strength of inference (Moll et al. 2017, Prugh et al. 2019). 2) Larger vertebrates can support many biologging technologies and long deployments, allowing for extensive observations across behavioral states during predator–prey interactions (Kays et al. 2015, Wilmers et al. 2015). 3) Context-dependencies in these taxa are known to influence the strength and nature of the non-consumptive effects of predation risk (Sheriff et al. 2020a, Wirsing et al. 2021), yet are also profoundly understudied (Say-Sallaz et al. 2019). Although we focus our attention on larger bodied vertebrates, we note that all elements of predator–prey theory discussed here are built upon and relevant to other taxa, which have served as the foundation for much of what is known about predator–prey ecology (Kotler 1984, Sih 1984, Hugie and Dill 1994, Brown et al. 1999). Additionally, we focus primarily on the actual risk of predation, but note that many of the same ecological and environmental contingencies described below will also impact prey's perception of predation risk (see section on evaluating nonconsumptive effects in free-ranging prey, below), which may in turn affect their behavior and contribute to the cumulative impact of predators (Gaynor et al. 2020, Allen et al. in press).

Overall, our review contributes a comprehensive analysis of the key realities that lead to disconnects across the predation sequence, with insights on issues that can, if not considered

carefully, result in inappropriate or inaccurate inferences when extrapolated across stages of the sequence. We argue that considering these key realities is particularly critical in anticipating and managing for changes in species interactions under the rapid environmental changes characteristic of the Anthropocene (Sih et al. 2016, Guiden et al. 2019). We discuss how a mechanistic understanding of encounter rates and capture probability will contribute to species conservation in the face of widespread global change, including invasive species establishment, landscape modification and pervasive anthropogenic stimuli.

## Linking overlap to predator–prey encounter rates

For a predator to encounter and subsequently capture a prey animal, both players must co-occur in space (Lima and Dill 1990). Thus, spatial overlap has been a defining metric in the spatial games of predators and prey (Sih 1984). Predator locomotion and hunting modes (e.g. sit-wait versus active search) have significant effects on how predators and their prey are predicted to use space (Schmitz et al. 2017), but the general assumption has been that predators should try to increase their overlap with prey while prey should try to minimize overlap in what is often called the ‘predator–prey space race’ (Sih 1984, Hugie and Dill 1994). The focus on spatial overlap as a proxy for predator–prey interactions, particularly in free-ranging animals, has been driven in large part by past practicalities (e.g. data availability and resolution, available statistical tools) and the difficulty of observing fine-scale movements and interactions directly. As such, predator–prey overlap has been assessed using readily available telemetry and camera trap data by quantifying co-occurrence (Courbin et al. 2009, Muhly et al. 2011, Gagné et al. 2016), home range or utilization distribution overlap (Courbin et al. 2013), or similarity of habitat use or selection (Basille et al. 2013, Smith et al. 2019a). However, the utility of quantifying spatial overlap to characterize predator–prey interactions is diminished if overlap is not a strong predictor of encounter probability. Potential disconnects between overlap and encounters may stem from at least three primary factors: 1) the degree of not just spatial, but *spatiotemporal* overlap; 2) species- and population-level characteristics affecting realized encounter rates; and 3) scales and concentrations of overlap (Fig. 2).

### Spatiotemporal overlap

The space race between predators and prey has a temporal dimension, given that overlap must occur in both space and time in order for an encounter to occur (Fig. 2a; Azevedo et al. 2018, Kohl et al. 2018). Prey activity patterns can decrease encounters in areas of high spatial overlap if prey utilize ‘predator downtimes’ to exploit areas of shared space use with predators (Kohl et al. 2018, Smith et al. 2019b). In this case, predators that are more constrained in their temporal hunting patterns (e.g. those that depend on

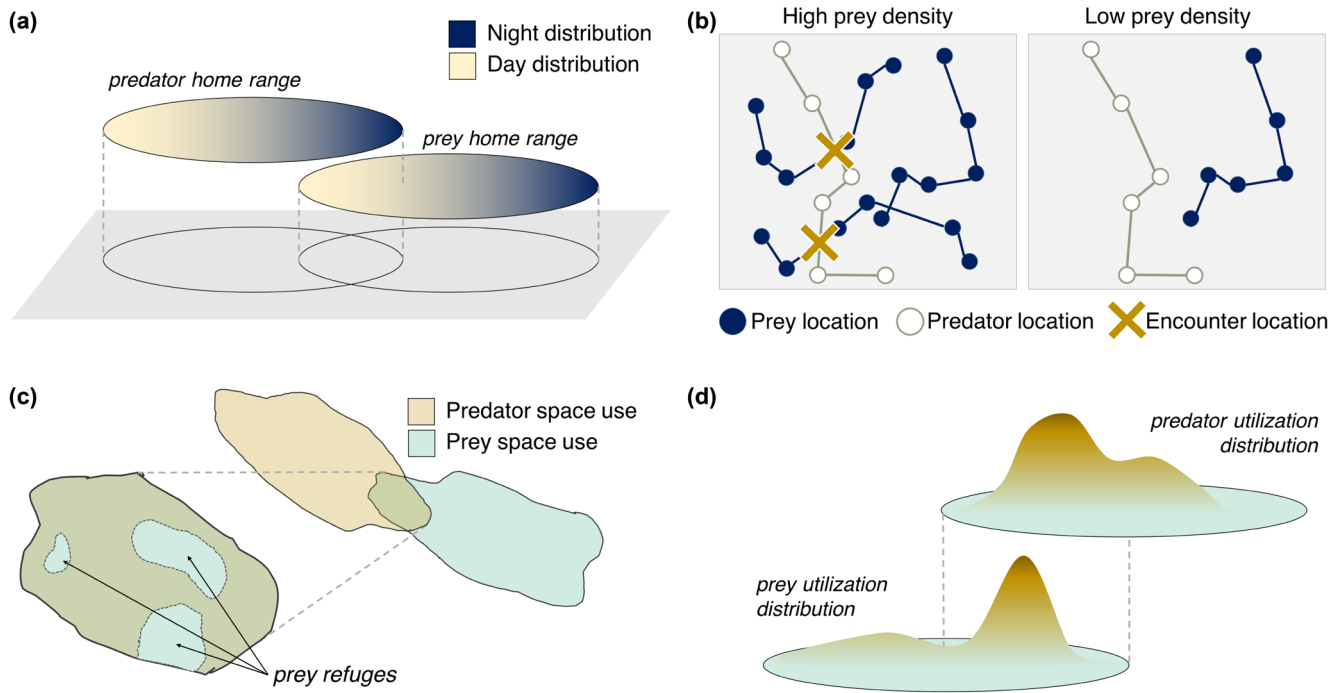


Figure 2. Contexts that contribute to disconnect between predator–prey spatial overlap and encounter probability. (a) Temporal overlap can increase or diminish encounter probability in areas of high predator–prey overlap; here, a prey animal primarily uses the overlap area during the day, while a predator uses the overlap area at night. (b) Prey density can have a positive relationship with encounter rates, particularly if predators overlap with multiple prey individuals that move independently. (c) Encounter probability varies across scales of overlap; within an area of shared space use, prey may be able to avoid encounters with predators through use of refuges (i.e. safe habitat). (d) The concentration of overlap has implications for encounter rates, whereby predator and prey utilization distributions may be highly overlapping due to a joint spatial anchor (e.g. a spatially limited resource such as a watering hole used by both predator and prey), even with limited spatial overlap.

a nocturnal hunting strategy to avoid being detected) may be hindered in their ability to maximize encounter rates by prey that have flexible activity patterns. Conversely, constraints on prey temporal activity can increase the correlation between overlap and encounters by allowing predators to more effectively track prey in time. Such constraints could include sensory limitations (e.g. visual foragers must be active during the day, thus increasing overlap with diurnal predators), other competitors or predators (e.g. avoiding a dangerous nocturnal predator may increase overlap with a diurnal predator), or thermal limitations (e.g. prey are constrained to be active during times of day or seasons that correspond with their preferred temperature range) (Monterroso et al. 2013, Bennie et al. 2014). Camera traps deployed throughout a study area can provide data amenable to recent advances in spatiotemporal modeling, including multi-species models, time-to-event models and avoidance–attraction ratios (Table 1) (Parsons et al. 2016, Karanth et al. 2017, Niedballa et al. 2019). Such methods allow researchers to quantify patterns of predator–prey co-occurrence in both space and time, though camera-based methods rarely capture encounter events directly. Biologgers (e.g. telemetry devices and other animal-borne sensors) can also be used to estimate temporal overlap in activity patterns from movement rates (Kohl et al. 2018, Smith et al. 2019b).

### Species- and population-level characteristics

Regardless of the degree of spatiotemporal overlap, higher predator or prey densities tend to increase individual encounter rates (Fig. 2b; Travis and Palmer 2005, Martin et al. 2018). Thus, encounter rates should typically be lower in low-density, unproductive systems than in high-density, productive systems (Sih 2005, Sims et al. 2006). Simple random encounter models (Gerritsen and Strickler 1977) add the basic insight that encounter rates should be higher when prey or predators exhibit higher movement speeds, and/or have larger encounter radii (including detection and recognition). In addition, mobility and detectability can interact in important ways. If highly mobile predators or prey are also highly conspicuous (i.e. have large encounter radii), then the combination can further enhance encounter rates. Insights from random encounter models, however, may be reversed when prey and/or predators respond to each other. For example, when prey actively avoid predators, high prey mobility and movement rates should reduce encounter rates (Sih 1984). Conversely, if predators are mobile and attracted to prey, and if prey are conspicuous and easily detected, this can lead to high encounter rates (Sih 1982). Thus for any given level of overlap, understanding the many organismal (e.g. locomotor capacity, motivations, sensory abilities) and environmental (e.g. landscape features, habitat modification) factors that

Table 1. Technological and statistical approaches to resolve the complexities of predator–prey interactions.

Research objective	Data source	Response variable	Statistical approach	Assumptions and limitations	Empirical examples
Overlap Spatial	Repeated surveys (camera trap, point count, etc.)	Co-occurrence of predator and prey at the same survey location	Co-occurrence occupancy models with dominant-subordinate species pairs (Waddle et al. 2010) or multispecies interactions (Rota et al. 2016); Joint species distribution models (Tobler et al. 2019)	Spatial overlap only; some methods require a priori assumption about which species drives overlap	Multispecies occupancy models reveal that invasive grey squirrels <i>Sciurus carolinensis</i> avoid pine martens <i>Martes</i> <i>maries</i> more strongly than do native red squirrels <i>Sciurus vulgaris</i> (Twining et al. 2021)
	Animal location data (e.g. VHF, GPS)	Percent overlap between predator and prey home ranges; shared resource selection	Statistical estimate of home range (HR) overlap (Winner et al. 2018); resource selection functions (Courbin et al. 2013)	Calculating error around HR overlap estimate is non-trivial; may be unclear over what time span to calculate HR and overlap; shared resource selection is a course estimate of overlap	Co-occurrence between wolves <i>Canis lupus</i> and their ungulate prey assessed based on shared resource/habitat selection (Courbin et al. 2009)
Temporal	Camera trap data	Correspondence between timing of predator and prey detections	Kernel density overlap coefficient (Ridout and Linkie 2009)	Sites are typically pooled, so spatial overlap is not incorporated	Sumatran tiger <i>Panthera</i> <i>tigris sumatrae</i> prey preference estimated based on temporal overlap with multiple prey species (Allen et al. 2020)
	Animal location data (e.g. GPS)	Correlation of movement rates	Generalized additive models (GAM) with cyclic regression spline (Kohl et al. 2018)	Movement rates are reflective of likelihood of encounter or predation risk	Correlation of cougar <i>Puma</i> <i>concolor</i> and vicuña <i>Vicugna vicugna</i> movement rates across the diel cycle (Smith et al. 2019b)
Spatiotemporal	Camera trap data	Time interval between predator and prey detections at the same camera site	Time-to-encounter models (Niedballa et al. 2019); avoidance–attraction ratios (Parsons et al. 2016)	Camera-based methods rarely capture actual encounters	White tailed deer <i>Odocoileus virginianus</i> spatiotemporal avoidance of coyotes <i>Canis latrans</i> and humans (Parsons et al. 2016)
	Animal location data; proximity sensors	Predator–prey encounter events	Proximity thresholds; multiple modeling approaches to detect intersections between movement paths (e.g. brownian motion/mass action (Martinez- Garcia et al. 2020), agent-based models (Baggio et al. 2011))	Sensitive to number of animals collared and the interval between relocations; require assumptions about how close paths must come to qualify as encounter (crossing? range?)	Wolf <i>Canis lupus</i> and elk <i>Cervus elaphus</i> encounters estimated as < 1-km distance between GPS locations (Middleton et al. 2013)

(Continued)



Table 1. Continued.

Research objective	Data source	Response variable	Statistical approach	Assumptions and limitations	Empirical examples
Classifying predator hunting/foraging to quantify risky encounters	Location data, accelerometers, magnetometers, depth sensors	Number of predator locations or proportion of movement path classified as hunting or foraging	Multiple modeling approaches to identify behavioral states from location data (e.g. k-means clustering (Van Moorter et al. 2010), BCPA (Gurarie et al. 2009), hidden Markov models (Adam et al. 2019)) and/or other logging data (e.g. recharge dynamics (Hooten et al. 2019), machine learning algorithms (Nathan et al. 2012))	Substantial data requirements to accurately identify behavioral states	Flight/dive patterns used to detect hunting/foraging behavior in Cory's shearwaters <i>Calonectris borealis</i> (Paiva et al. 2010) and imperial cormorants <i>Phalacrocorax atriceps</i> (Gómez Laich et al. 2012); 'recharge dynamics' model used to determine hungry versus satiated states in cougars <i>Puma concolor</i> (Hooten et al. 2019)
Detection Predator detection events by prey	Heart rate monitors, acoustic monitors	Changes in prey behavior/physiology indicative of a predator detection; time allocation to vigilance behavior	Regression models to assess ecological covariates associated with changes in behavior/increased vigilance (Lynch et al. 2015)	May require additional data inputs (e.g. predator location data) to determine whether physiological/behavioral changes are driven by predator detection or other changes in perceived risk (e.g. moving from refuge to open habitat)	Narwhal <i>Monodon moneros</i> detection of seismic blasts (which induce antipredator behavior) detectable from changes in heart rate (Williams et al. 2017) 'acoustic vigilance' (i.e. pauses in cud chewing) by mule deer <i>Odocoileus hemionus</i> when predators present (Lynch et al. 2015)
Attack, capture and kill Predator attack rates on prey	Location data, accelerometers, magnetometers, gyroscope	Occurrence/frequency of attack events	Activity profiles (Williams et al. 2014) used to identify events of exceptionally fast movement/high acceleration/sharp turning angles associated with predator chases/attacks	Substantial data requirements to accurately identify attack events	White shark <i>Carcharodon carcharias</i> predation attempts detected from lateral speed, tail beat frequency and pitch angle (Watanabe et al. 2019); Distinct biollogging signatures for stalk, chase and pounce in cougars (Williams et al. 2014) and cheetahs <i>Acinonyx jubatus</i> (Wilson et al. 2013)

(Continued)

Table 1. Continued.

Research objective	Data source	Response variable	Statistical approach	Assumptions and limitations	Empirical examples
Capture success	(Paired) accelerometers, hall sensors, location data, acoustic monitors	Occurrence/frequency of capture or feeding events (indicative of successful hunt)	Feeding behavior (indicating capture success) identified from multiple data sources using, e.g. Gaussian mixture models (Wilmer et al. 2017), random forest models (Pagano et al. 2017)	Substantial data requirements to accurately identify capture or feeding events; may be difficult to discern feeding following successful hunt from scavenging (applies to GPS data, less to accelerometry or audio data)	Hall sensors detect mouth opening (prey capture) events by diving fur seals <i>Arctocephalus gazella</i> (Viviant et al. 2014); acceleration differences between head- and back-mounted accelerometers detect prey capture events by Adélie penguins <i>Pygoscelis adeliae</i> (Watanabe and Takahashi 2013); location and duration of African lions <i>Panthera leo</i> feeding events determined based on GPS and accelerometry data (Suraci et al. 2019a) or acoustic monitoring (Wijers et al. 2018)

affect movement distances, speeds and encounter radii can be crucial for explaining variation in encounter rates within an area of shared space use (Nathan et al. 2008, Hertel et al. 2020, Doherty et al. 2021). Advances in biologging data provide some of the most promising avenues for quantifying the effects of such organismal or environmental factors on encounter rates. Improvements in tracking technology (e.g. via GPS tags) now allow the reconstruction of predator and prey movement paths with high spatiotemporal resolution (Rafiq et al. 2020), and continuous-time movement models (Michelot and Blackwell 2019), validated with such high-resolution data, can provide a relatively complete picture of encounter rates (e.g. number of times movement paths were within the predator or prey detection range), at least for the subset of animals that are tagged. Additional biologging devices deployed on predators or prey, including acoustic or heart rate monitors, can be used to assess encounter radii through changes in animal behavior indicative of predator or prey detection (Lynch et al. 2015, Williams et al. 2017).

### Scales and concentrations of overlap

High spatiotemporal overlap at a large scale (e.g. overlapping predator and prey home ranges and matching seasonal activity patterns) can still yield low encounter rates if at finer scales predators and prey have concentrations of space use or temporal activity that do not heavily overlap. This scenario may occur if predator and prey have narrow and opposing habitat domains (i.e. feeding ranges) within large areas of shared space use (Schmitz et al. 2017). Analyses can account for issues of scale by calculating overlap not for the overall home range, but for home range centers (e.g. 50% KUDs) or full utilization distributions (Fieberg and Kochanny 2005). Prey use of refuges from predators within their home ranges (i.e. safe habitat where the likelihood of encountering a predator is relatively low) can lead to variation in encounter rates at even finer scales (Fig. 2c). Similar issues of scale are relevant for temporal overlap. Even if predators and prey are active in the same seasons (large temporal scale), encounter rates may nonetheless be moderate to low if predator and prey partition space within the diel cycle (small temporal scale) (Courbin et al. 2019). Importantly, fine scale avoidance by prey of risky times or places (Creel et al. 2008) may result in nonconsumptive effects of predation risk on prey. Improvements in the reliability and resolution of GPS location data (Bastille-Rousseau et al. 2016, Smith et al. 2020a), along with methods for quantifying diel activity patterns of predators and prey (Ridout and Linkie 2009), will help to resolve these fine-scale patterns of spatiotemporal overlap.

An alternative outcome involves concentrated bursts of overlap within small areas of shared space use that can result in high encounter rates, which may in turn lead to high predation risk (Fig. 2d). For example, if prey have 'spatial anchors' (Sih 2005, Smith et al. 2019a) such as watering holes, lekking grounds or a limited number of patches with high resource availability, the spatial (and temporal) predictability of prey presence may allow predators to anticipate their occurrence at

specific times and places, giving predators ready access to prey despite overall low spatiotemporal overlap. Notably, in these predictable situations, even if overall encounter rates are not high, predation can be high if the encounters occur in situations with high predation success (i.e. high CCP). Greater understanding of environmental characteristics that act as spatial anchors (e.g. resource concentrations) and/or affect predator hunting success (e.g. vegetation cover) is increasingly available from high-resolution remote sensing data on habitat structure (Suraci et al. 2020) and fine-scale 3D reconstructions of the environments in which predator–prey interactions take place (Olsoy et al. 2015).

The aforementioned considerations are vital for assessing the link between predator–prey overlap and encounter probability. In addition to these considerations, a complete enumeration of overlap and encounters requires having simultaneous data on all individuals in a population or subpopulation, a major challenge due to the difficulty of continuous observation throughout diel and annual cycles, and because financial, operational and animal welfare logistics usually preclude placing monitoring devices on entire populations or certain species (e.g. critically endangered species). However, emerging technologies that facilitate tag miniaturization (Ripperger et al. 2020), and low-cost global tracking networks (Curry 2018), are poised to substantially increase our capacity to simultaneously monitor large numbers of

predator and prey individuals, providing further insights into the nuances of predator–prey overlap and encounter.

## Linking encounter rates to conditional capture probability

Measuring encounter rates, as discussed in the previous section, is most valuable to understanding predator–prey dynamics if variation in encounters provides strong insights into the probability of prey being killed by the predator. However, predation risk depends on both encounter probability and the probability of capture given an encounter (i.e. conditional capture probability, CCP) (Hebblewhite et al. 2005). Like the relationship between overlap and encounter rates detailed above, the relationship between encounter and capture probabilities (and, as such, the variability in CCP) depends on features of both the environment and the predators and prey (Fig. 3). Even where encounter rates are high, CCP and thus overall predation risk can be low if 1) predators are not actively hunting; 2) predators are actively hunting but choose not to attack prey, even when they are likely to be successful; or 3) predator success in capturing prey is low because of environmental circumstances or prey traits. These conditions determine whether a predator–prey encounter poses direct lethal risk to the prey, i.e. a risky encounter.

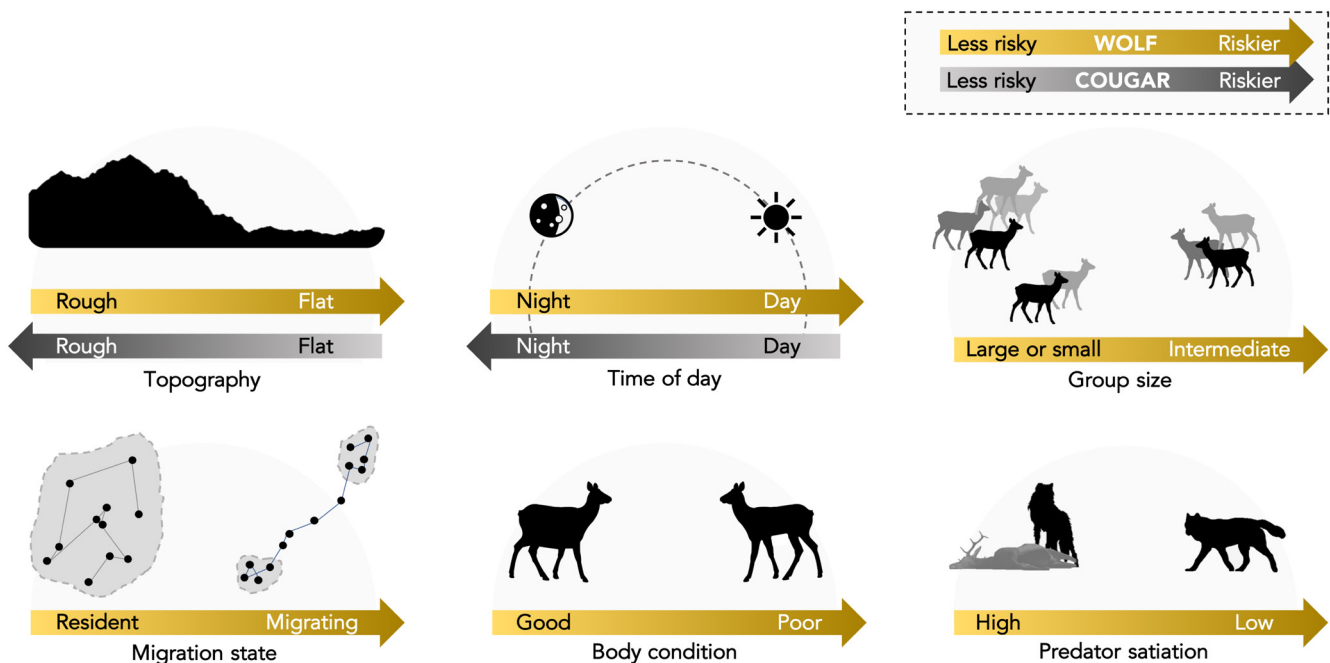


Figure 3. Predator–prey encounters are not always risky for prey animals if the conditional capture probability (CCP) is low due to intrinsic or extrinsic conditions. Context-dependency in a well-studied ungulate, the elk *Cervus canadensis*, has been demonstrated to affect the riskiness of encounters with predators, particularly in relation to environmental features (e.g. topography, time of day; Kohl et al. 2019), prey state (e.g. group size; Hebblewhite and Pletscher 2002), migration state (Hebblewhite and Merrill 2007, Robinson and Merrill 2013), body condition (Creel et al. 2007, Winnie and Creel 2007), predator state (e.g. satiation; Liley and Creel 2008), predator identity (e.g. species, hunting mode; Kohl et al. 2019), and the interactions between these conditions. In elk, for example, an encounter with a wolf *Canis lupus* in rugged terrain would be relatively less risky, whereas an encounter with a cougar *Puma concolor* in rugged terrain would be relatively riskier. All examples shown here have been documented in the literature on wolf–elk and cougar–elk interactions.



## Predator hunting state

Perhaps the simplest reason for low CCP is that predators are often not actively hunting because they have recently fed and are satiated (Fig. 3). If predators are often satiated, high encounter rates should not translate into high risk to prey (i.e. many encounters are not risky), and it has been shown that prey respond differently to hungry or not hungry predators (Berger-Tal and Kotler 2010). We predict that this scenario (low risk despite high encounter rates) is more common for predators that: 1) feed on prey that are large relative to the predator body size; 2) have low metabolic needs (e.g. many ectotherms in cool temperatures); or, 3) enjoy high resource availability and prey choice (e.g. many avian predators have a plethora of small vertebrate species within their home range). Predators may also not actively hunt when they have competing demands (e.g. when mesopredators are vigilant to reduce risk from larger predators, or when predators are engaged in mating, communication or territorial behaviors). To quantify if predators are in an active hunting behavioral state and incorporate this information into analyses of predator-prey interactions, advances in biologging technology (e.g. accelerometers, magnetometers, gyroscopes, animal-borne cameras; Table 1) can be used to identify when predators are hunting rather than engaged in other activities (Wilson et al. 2013, Viviant et al. 2014, Williams et al. 2014, Wang et al. 2015). Furthermore, integrating data from multiple biologging devices could be used to combine estimates of feeding behavior (Suraci et al. 2019a) and energetic demands (Nickel et al. 2021), allowing for predictions of when a predator should engage in hunting behavior following a kill event.

## Predator dietary preference

Even when predators are actively hunting, they might not choose to attack a specific prey animal if searching for more profitable prey. Secondary (i.e. less preferred) prey may thus be less likely to respond to encounters than primary prey. However, understanding whether a species is a primary or a secondary prey relies on quantification of numerous factors; presence in diet will likely reflect predator intrinsic preferences and experience, prey relative availability and prey ability to escape encounters and attacks (Sih and Christensen 2001). Many established technological approaches are available to estimate the two latter factors (e.g. camera trap or community science data for prey availability, biologging for prey response, Xiao et al. 2018, Kafley et al. 2019). To investigate predator preferences, diets can be quantified using novel methods that can increase resolution and confirm individual identity, including stable isotope (Robillard et al. 2017, Larson et al. 2020) and DNA metabarcoding diet analyses (Shehzad et al. 2012, Smith et al. 2018, Ando et al. 2020). Assessments of predator diet and prey selection can also be facilitated by predator head-mounted accelerometers or video cameras (Watanabe and Takahashi 2013, Watanabe et al. 2019), though low encounter rates and logistical issues with battery life and data storage and processing

continue to present challenges. Combining information on prey density and antipredator behavior with diet data (e.g. from kill site field investigations, biologging devices, stable isotope analyses or DNA metabarcoding) should allow a clearer understanding of predator dietary preferences and their effects on CCP.

## Predator hunting constraints and prey traits

Finally, CCP can be low if predators have low lethality given the environmental conditions; efficacy of prey escape, hiding and physical defenses; or an interaction between the two (Fig. 3). Many encounters are not risky because they occur during times or in places in which predators have low probability of capture given an attack. Particularly for predators that rely on stealth, such as ambush or stalking predators, CCP can be lower in times and places of high visibility, such as during the day (Smith et al. 2020a) or in open habitats (Davidson et al. 2012). These patterns may be strongest for prey that rely on vigilance as their primary antipredator strategy. While behavioral ecologists have long sought to quantify antipredator behavior (e.g. vigilance, small-scale refuge use) via direct behavioral observations, this can be difficult to do continuously, particularly with secretive, mobile prey (although camera traps can be used to examine prey behavior (Smith et al. 2020b)). Technological and statistical advances, such as using head-mounted accelerometers to determine behaviors from an 'orientation sphere' (Wilson et al. 2020) or auditory biologgers that can delineate prey behaviors (Lynch et al. 2015, Studd et al. 2019), allow for continuous information on relevant prey behaviors such as vigilance and feeding rates. In addition to vigilance, prey may use camouflage, small scale refuge use and locomotive escape tactics (Wilson et al. 2018) to reduce CCP. To better quantify factors that influence prey escape success, recent studies have used video (including drones with video cameras), accelerometers on predators and prey, or satellite imagery (to map sightlines or escape lines) (Olsoy et al. 2015, Davies et al. 2016).

The above examples reflect how high encounter rates may be decoupled from overall predation risk due to low CCP. However, there may also be circumstances where overall risk is elevated in low-encounter times or places due to high CCP. Variation and distribution of CCP may be most important for ambush predators or for cursorial predators in conditions that limit escape. These conditions may arise from disturbance events (e.g. fire) or anthropogenic impacts (e.g. land-clearing or urbanization) that modify habitats in such a way as to facilitate the easier capture of prey by predators (Fleming and Bateman 2018, Nimmo et al. 2019, Fležar et al. 2019). Such changes have important conservation and management implications, as discussed below. For predator-prey systems in which CCP drives patterns of habitat use and activity, ecologists should limit inferences made from spatial overlap alone and instead focus on identifying factors that affect the frequency of particularly high-risk situations.

## Broader implications of complexity in predator–prey interactions

Reducing our reliance on proxies for predation risk, like simple metrics of spatial overlap, and better integrating the ecological and environmental complexities described above into predator–prey interactions studies will have multiple benefits for both fundamental and applied aspects of predator–prey ecology. A better understanding of the complexity of predation risk will help to resolve questions regarding the strength of nonconsumptive effects of predators on prey and inform conservation and management strategies. The emergence of new empirical findings on the nuances of predator–prey interactions among free-ranging animals, made possible by technological advances, can improve quantitative predictions about dynamic predator–prey systems and generate new avenues for empirical research.

### Evaluating nonconsumptive effects in free-ranging prey

Antipredator behaviors and other responses (e.g. morphological changes) that are employed by prey animals to reduce predation risk (either by reducing predator encounter or conditional capture probabilities) often have physiological costs (e.g. energetic costs of escape, increased stress) and opportunity costs (e.g. reduced feeding rates, lost mating opportunities) (Sheriff et al. 2020a, Wirsing et al. 2021). Nonconsumptive effects (NCE) of predation risk occur when these costs negatively impact prey abundance or fitness (Peacor et al. 2020). Hundreds of studies have documented NCEs in laboratory settings (Preisser et al. 2005) or experimentally in the field (Zanette et al. 2011, Allen et al. in press). These studies have suggested numerous hypotheses on how prey, predator and environmental characteristics might influence the strength of NCEs in nature (Sheriff et al. 2020a, Wirsing et al. 2021). However, few studies have rigorously quantified the connection between antipredator behaviors and NCEs in free-ranging, highly mobile animals (Say-Sallaz et al. 2019). New methods that are improving our understanding of antipredator responses and predation risk can also enhance our understanding of NCEs in nature and thus help us to refine and test hypotheses on factors influencing variation in NCEs.

A general assumption has been that stronger antipredator behaviors produce stronger NCEs. Mis-assessments of NCEs can occur, however, if antipredator behaviors are measured at too coarse a scale. For example, even if prey generally avoid predators in both space and time, NCEs can be low if prey have windows of safety during which they can exhibit concentrated, compensatory feeding (Sheriff et al. 2020a). Furthermore, the magnitude of the trait response to perceived predation risk should be a function of the frequency of exposure to risk cues, as predicted by the Risk allocation hypothesis (RAH; Lima and Bednekoff 1999). The RAH predicts that prey will exhibit the strongest responses (e.g. greatest increase in vigilance at the expense of foraging) during brief periods of perceived risk in an otherwise relatively safe

environment and that, because of the need to meet energetic demands through foraging, responses to immediate risk will be lower in environments with more frequent risk (Lima and Bednekoff 1999, Creel et al. 2008). Thus, assessing perceived risk from observed antipredator behaviors alone may provide an inaccurate depiction of risk perception and any NCEs resulting from reduced foraging or changes in habitat use. Continuous monitoring of encounter rates and CCP may be necessary to accurately discern levels of risk perception and to contextualize NCEs against the background level of risk across stages of the predation sequence.

Conversely, even if prey do not appear to avoid predators at a large scale (i.e. predators and prey exhibit high spatio-temporal overlap), a large NCE may emerge if, at a smaller scale, prey: 1) are restricted to foraging near refuges, 2) forage inefficiently when vigilant or 3) experience physiological impacts (e.g. from stress). Notably, if prey have poor information about predator location or behavior, the cost of under-responding can cause prey to over-avoid predators at both small and large scales and thus suffer strong NCEs (Luttbeg and Trussell 2013). Emerging technologies allow researchers to better study these possibilities in nature by evaluating prey and predator behaviors continuously at fine scales in space and time (e.g. with GPS, accelerometers or magnetometers (Wilson et al. 2018, 2020)) throughout the predation sequence. Taking full advantage of technological advances to examine NCE strength will require investigation of the relationship between the full suite of employed antipredator behaviors (e.g. vigilance, movement behavior, feeding rates and habitat selection) and potential associated fitness measures (e.g. pregnancy rate, birth rate, recruitment, age-specific survival and population growth rate).

### Conservation and management implications of predator–prey interactions

The rapid environmental change and novel ecological conditions characteristic of the Anthropocene (Sih et al. 2016, Guiden et al. 2019) are altering species interactions by reshuffling predator–prey communities and reshaping the landscapes on which interactions occur. A better understanding of the factors influencing the predation sequence and its ecological outcomes may help decision-makers prioritize what conservation interventions are most needed, where they should be located, and assess their likely efficacy. Pressing conservation issues that require a more mechanistic understanding of predator–prey interactions include invasive species control; habitat management, restoration and augmentation; and mitigating the impacts of anthropogenic disturbance, including noise and light pollution.

#### *Invasive species*

The degree to which invasive predators impact local wildlife populations is affected by their ability to both encounter and successfully capture native prey (Moseby et al. 2015, Carthey and Blumstein 2018). Understanding at which stage of the predation sequence prey are most vulnerable to invasive

predators can inform how to prioritize costly and intensive conservation action. For example, if prey risk high encounter rates with predators, managing habitat structure (e.g. openness related to fire and/or grazing regimes) may reduce overall predation risk (Doherty et al. 2015, Geary et al. 2020). Conversely, if high CCP is a greater risk to prey due to predator naivety, managers can train prey to better identify dangerous invasive predators (Blumstein et al. 2019).

### **Habitat modification**

Habitat structure and distribution affect interactions across the predation sequence including detection distances, refuge availability and escape terrain, which interact with the sensory and performance capabilities of predators and prey (Wheatley et al. 2020). Ongoing changes in land cover through habitat fragmentation and the spread of invasive plants will affect both encounter rates and capture probability by reshaping the playing field on which predator–prey interactions occur (Mattos and Orrock 2010, Penn et al. 2017). Environmental policy and land management practices (e.g. sustainable grazing, appropriate fire regimes) that prioritize the preservation or restoration of habitat attributes, such as structurally complex vegetation cover, may promote coexistence of predators and prey (McHugh et al. 2019, Miritis et al. 2020, Stobo-Wilson et al. 2020). Direct habitat manipulation, such as by providing artificial shelters for prey to seek cover from predators (Bleicher and Dickman 2020), can be used as an interim measure as habitats recover post-disturbance (e.g. fire).

### **Anthropogenic stimuli**

Anthropogenic development, including housing, resource extraction and roads, introduces noise and light pollution that can affect species interactions (Fleming and Bateman 2018). Light pollution can increase detection by predators or prey, increasing encounters and either increasing or decreasing CCP (Ditmer et al. 2021). In contrast, noise pollution masks auditory cues and can therefore decrease detection by predators or prey, decreasing encounters or increasing CCP (Francis and Barber 2013). To reduce the impacts of noise or light pollution on encounter and predation between native predators and prey, managers can mandate reduced noise or light in target areas or times of day during which native species are particularly sensitive to predation risk (Dominoni et al. 2020). Conversely, managers may suggest manipulating noise or light disturbance to give a native species an advantage over its invasive or overabundant predator or prey.

Perceived risk from humans themselves may also influence multiple stages of the predation sequence by altering predator and prey behavior and space use (Kuijper et al. 2016, Suraci et al. 2019b). Where prey are more tolerant of people than are predators (e.g. because predators are at greater risk of mortality from humans), anthropogenic activity may lead to reduced spatial overlap and/or encounter rates if prey preferentially use areas of high human presence (Muhly et al. 2011). Alternatively, human activity may benefit predators in situations in which chronic exposure to human cues (e.g.

through high levels of ecotourism) leads to generalized habituation in prey, thus increasing CCP by reducing prey responsiveness to the cues of actual predators (Geffroy et al. 2015). Managing the intensity of human activity (e.g. by restricting recreational activity at certain times or places) may therefore be necessary to promote natural levels of predation and/or reduce the impacts of invasive predators on prey.

### **Integrating mechanistic understanding into predator–prey theory**

Ideally, empirical work should suggest key aspects of reality to add to theory, and the augmented theory should then generate predictions for empiricists to test. Thus, the data from new technologies and statistical methods should facilitate a powerful new theory–empirical loop. Game-theoretic models, in which predators and prey respond adaptively to each other, have noted the likely importance of constraints (e.g. on relative mobility or information) or ‘anchors’ (e.g. the need for prey to forage on their own resources) on the space use of predators and prey (Patin et al. 2020), but wildlife studies have generally not modeled these issues explicitly. Future models should add the key contingencies highlighted throughout this review, draw on new field data to estimate model parameters, and produce predictions that are now more testable given the advances in data collection approaches. A better understanding of factors underlying encounter rates and conditional capture probabilities in nature should guide models to include these dynamic realities that predict predation rates, predation risk effects and the resulting trophic dynamics. The time is ripe for new data and theory to reshape how predator–prey interactions are conceptualized, modeled, studied and quantified in natural landscapes.

### **Conclusions and future directions**

We suggest that emerging technologies and statistical methods are facilitating a transition to a more spatiotemporally detailed, mechanistic understanding of predator–prey interactions in nature, allowing for the concurrent examination of multiple stages of predator–prey interactions in highly mobile, free-ranging animals. Nonetheless, many studies on mobile animals continue to rely on an earlier framework focused on the predator–prey space race under the assumption that the degree of spatial overlap should be informative about the overall predator–prey interaction. However, both theory and recent empirical work suggest that this simplification does not always hold. Here, we emphasize that the link between spatial overlap and predation risk depends on both: 1) whether spatial overlap predicts encounter rates, and 2) whether encounter rates then predict prey capture. To predict encounter rates, a scale-dependent understanding of spatiotemporal overlap and more detailed movement patterns (including the predictability of those movements) in space and time are essential. Variation in predation risk also depends on CCP, which can distinguish benign encounters



from risky ones. By employing the methodological advances described in this review and summarized in Table 1, ecologists can compile data across species and ecological contexts to identify which stage(s) in the predation sequence and which ecological contingencies are most critical in determining the outcome of predator–prey interactions, with benefits for both ecological theory and ecosystem conservation.

The next challenge is to develop a more complete conceptual framework for understanding factors that explain variation in overlap, encounter rates and CCP. The characteristics of predators and prey themselves are likely to be major sources of variation. For instance, animal energy stores, hunger levels and reproductive state are known to be key drivers of behavior and space use (Hooten et al. 2019), including risk-taking behavior in prey. How state-dependent decision making by predators and prey affects encounter rates and conditional capture probability remains an important unanswered question. Prey personalities may also affect the relative importance of avoiding encounters versus avoiding capture if, for instance, bolder individuals, whose behavior may lead to higher encounter probability with predators, specialize in detecting or escaping predators while shyer individuals rely more on crypsis and avoiding encounters in the first place. In addition to individual-level variation, the environmental context, including both biotic (e.g. community composition) and abiotic factors (e.g. landscape features that affect detection or capture success) will likely affect the links between overlap, encounter and capture success. A key question is to what extent insights regarding encounter rates and CCP from single predator–prey pairs apply to multi-predator, multi-prey systems. More generally, how does the community context (e.g. presence of multiple predators and competitors) alter predictions regarding overlap, encounter and capture success? Each of these questions represents an important avenue for future research and application. The research methodologies are now available to facilitate these important new directions in predator–prey ecology. We urge our field to build upon the founding framework of the space race and predator–prey overlap to examine predictors of the full predation sequence and their impact on predator–prey interactions.

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## Author contributions

**Justin P. Suraci** and **Justine A. Smith** contributed equally to this publication. **Justin P. Suraci**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing

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## Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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